

A FAUNAL REVIEW OF THE JUDITH RIVER (OLDMAN) FORMATION,
DINOSAUR PROVINCIAL PARK, ALBERTA

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Abstract

The Upper Cretaceous (Campanian) Judith River (Oldman) Formation of southern Alberta has yielded the richest dinosaur fauna known from anywhere in the world. Dinosaurs have been described from Dinosaur Provincial Park since 1902, and new genera continue to be described up to the very present. The 28 genera currently recognized as valid exceed by more than 50% the number of genera of dinosaurs occurring in the Morrison Fm. of the western United States (18 at all sites combined) and the Nemegt Fm. of Mongolia (16 genera). The fauna is dominated by hadrosaurs, followed by ceratopsians, ankylosaurs, tyrannosaurs, pachycephalosaurs, small theropods, and ornithomimids, in that order. Each group of dinosaurs is reviewed with respect to its taphonomy, relative abundance and inferred ecological role. The bias of the fossil record against the preservation of articulated remains of small animals is emphasized, with particular reference to pachycephalosaurs, small theropods and crocodilians. This study shows that, far from being rare, Stegoceras, the small pachycephalosaurid, is actually the most abundantly represented genus among the generically diagnostic remains of all the dinosaurs. The contribution of non-dinosaurian vertebrates to the fossil record is reviewed, and prospects for recreating paleoecological trends over a wide geographic area are outlined.

Introduction

The Upper Cretaceous Judith River (Oldman) Formation of southern Alberta provides one of the richest dinosaur faunas in the world. Although numerous fossil-producing localities are known around the province, the most important by far is Dinosaur Provincial Park (DPP), situated on the Red Deer River 50 km northeast of Brooks. At this site, badland exposures along a 25 km stretch of river have yielded more than 300 specimens of complete or partial dinosaur skeletons that are currently referred to 28 genera. Probably no place else on Earth has produced more dinosaur skeletons, although more and larger bones come from the Upper Jurassic Morrison Formation of the western United States. From the Morrison Fm., 18 genera in all are recognized, but the number at any site never exceeds 13 (Dodson et al., 1980). The fauna at the very rich site of Tendaguru (Upper Jurassic) in Tanzania includes 10 genera (Galton, 1977).

From the Upper Cretaceous beds of Mongolia, only 8 genera are known from the Djadokhta Formation, source of the abundant primitive ceratopsian, Protoceratops; while 16 genera are known from the overlying Nemegt Formation (Osmolska, 1980). Nowhere are more different kinds of dinosaurs found than in Alberta. In recognition of such riches, the Park was named a World Heritage Site in 1980 by the United Nations Educational, Scientific and Cultural Organization (UNESCO).

In addition to dinosaurs, remains of clams, snails, plants, fishes, amphibians, non-dinosaurian reptiles (turtles, lizards, crocodiles, champsosaurs, plesiosaurs, pterosaurs), and mammals are found. Because of the richness of all of these, the Judith River (Oldman) Formation represents a standard against which all other dinosaur faunas are compared. The purpose of this paper is to review the fauna at Dinosaur Provincial Park. The comparatively well-studied dinosaur component and the less well-studied non-dinosaurian component will be reviewed separately. In addition, taphonomy of the fauna will be reviewed, based on current work by the author in cooperation with the Tyrrell Museum of Paleontology, Drumheller. A brief summary of past work is offered first.

History of Collection

L. S. Russell (1966) and Colbert (1968) give excellent accounts of the history of discovery of fossils in Alberta. The first important dinosaur find in Alberta was made in 1884 by Tyrrell of the Geological Survey of Canada; he discovered a partial skull of a large meat-eater in the younger (Maastrichtian) beds of the Horseshoe Canyon Formation (Edmonton Group) near Drumheller. This specimen was named Albertosaurus by Osborn (1905). In 1889, Weston of the Survey descended the Red Deer by boat and discovered the rich fossil beds at Steepleville and the Deadlodge Canyon, both areas included in Dinosaur Provincial Park today. Though he recognized the importance of the terrain, he collected little. Lawrence Lambe (whose name was honored in the duck-billed dinosaur Lambeosaurus) was the first Survey paleontologist to concentrate on collecting dinosaur fossils in the Judith River (Oldman), where he worked from 1898 to 1901. Scientific descriptions were soon forthcoming (Stegoceras, 1902; Centrosaurus, 1904; Euoplocephalus, 1910). The golden age of dinosaur collecting at the Park began in 1912 with the arrival of Barnum Brown from the American Museum of Natural History. Brown worked there until 1915 with spectacular success (Corythosaurus, 1914; Prosaurolophus, 1916; Struthiomimus, 1917). The Geological Survey of Canada hired C. H. Sternberg and his three sons, George, Levi, and C. M., and they arrived to work the Oldman in 1913 with equal success for several years (Styracosaurus, 1913; Chasmosaurus, 1914; Panoplosaurus, 1919). C. H. and Levi Sternberg left the Survey in 1916, and C. M. Sternberg alone worked the Survey (later the National Museum of Canada) for his entire career. Geological Survey of Canada/National Museum of Canada expeditions have continued intermittently over the years. In 1918 Dr. W. A. Parks of the Royal Ontario Museum initiated that institution's serious interest in dinosaur fossils, and worked continued there until 1921, and in many subsequent field seasons, most recently 1957. Results of this collection include the spectacular skull and skeleton of Parasaurolophus (1922) and Lambeosaurus (1923). In recent years the University of Alberta, led by Dr. R. C. Fox, collected there from 1967-1971; and today the Tyrrell Museum of Paleontology (formerly Provincial Museum of Alberta) has concentrated work there, beginning in 1979 and led by Dr. Philip J. Currie. Dinosaurs continue to be described from the Oldman (Saurornitholestes Sues, 1978; Gravitholus Wall and Galton, 1979; new pachycephalosaurid, Galton and Sues, 1983) and new skeletons continue to be found at the rate of half a dozen or more per year.

Sediments and Climate

Sediments of the Judith River Formation of Montana continue without interruption into southern Alberta; it therefore seems proper to recognize the priority of the older name over the more recent Oldman (McLean, 1977). The chronostratigraphic term, "Judithian," was proposed to designate the time interval during which the biota of these terrestrial formations lived (L. S. Russell, 1964). The term "Oldman local fauna" may be coined to specify the fossils found at the locations now included in Dinosaur Provincial Park, thus preserving the historically significant name, "Oldman" (D. A. Russell, pers. comm., 1982).

Sediments of the Judith River (Oldman) Formation at Dinosaur Provincial Park consist of poorly consolidated sandstones, siltstones, and drab mudstones containing variable, often large, amounts of plant material. Although plant material is abundant both in sandstones and mudstones, coals are rare, presumably because plant materials were continually diluted by the influx of sediment. Sandstones dominate the Park as a whole, constituting approximately 70% of all sediments. Cross-bedded sandstones have been identified as channel sandstones, and the dominance of channels and the disposition of channel sands relative to overbank (i.e., floodplain) deposits suggest that braided channels migrated laterally across the landscape (Dodson, 1971; Russell, 1977).

In late Campanian time, Dinosaur Provincial Park was situated some 320 km (200 miles) east of the rising Rocky Mountains and some 110 km (70 miles) west of the seashore (Dodson, 1971). Small vertebrates, invertebrates, and plants all suggest fresh-water conditions; however, the abundance of such euryhaline fishes as gars (Lepisosteus), sturgeons (Acipenser), and batoid, Myledaphus, suggests that the rivers passed directly into the sea. Interestingly enough, the articulated remains of plesiosaurs (?Leurospondylus Brown, 1913) reported only once from the Park (Lambe, 1902) until very recently, have now been found during each of the last three summers; a partial skeleton was excavated by the Tyrrell Museum in 1981. Although some might regard the existence of plesiosaurs as prima facie evidence of marine conditions, I believe that their sparse occurrence is fully compatible with the evidence presented by the freshwater and euryhaline organisms (Russell, 1931); just as certain whales and sharks do today, plesiosaurs occasionally entered estuaries and came upstream in search of novel food or perhaps to shed infestations of marine ectoparasites.

Geographic distribution of recent relatives of Judithian fishes, amphibians, reptiles, and plants suggests that the climate was warm temperate, or possibly subtropical. The seasonal nature of the climate is indicated by growth rings in trees and in teeth and vertebrae of cold-blooded vertebrates (Dodson, 1971; Johnston, 1979).

The Fossil Record

The fame of Dinosaur Provincial Park stems in large measure from the occurrence of large numbers of articulated specimens of dinosaurs. Quantitative studies of Judith River (Oldman) dinosaurs have drawn on a census base of 250 to 320 specimens (Russell, 1967; Béland and Russell, 1978). Until recently, almost all of the collecting from the Park sampled articulated specimens.

However, articulated specimens represent a distinctive taphonomic mode (or characteristic pattern of preservation) and a potentially biased population sample, however satisfying for esthetic purposes. For every skeleton in the Park, there are literally hundreds of bones, uncollected but identifiable anatomically, and taxonomically determinate at least at the level of family. Isolated bones represent a second distinct taphonomic mode, one reflecting a different set of preservational biases, and potentially complementing census data provided by the skeletal census. Bonebeds, concentrations of large bones (greater than 50 mm in length), often under specific sedimentary conditions (e.g., clay-sand interfaces), are abundant in the Park and represent a third taphonomic mode. Since 1980, more than 80 bonebeds have been identified (Currie *et al.*, 1981), and systematic studies are now underway. Bonebeds vary greatly in size, density, and faunal composition. One of the richest of these, Quarry 143, covers 2,000 m² at an average density of 20 bones/m² (Currie, 1981; Currie and Dodson, MS). This bonebed is dominated by a single genus of ceratopsian, *Centrosaurus*, with juvenile, subadult, and adult individuals. Other bonebeds demonstrate greater taxonomic diversity. Some bonebeds cover distances of a kilometer or more laterally at low bone density. A fourth taphonomic mode are the so-called microfauna accumulations, apparent hydraulic or biological concentrations of the most resistant remains (teeth, scales, plates, vertebrae) of small vertebrates (average bone size about 11 mm). Microfaunas are important because they sample the elusive small component of the vertebrate fauna. Specialized bulk-processing techniques using dry and wet screening and sorting of the resultant residues under binocular microscope extract rare mammalian or herpetological specimens. However, in the Park, microfaunas average 37% dinosaurian material (ranging up to 54%), particularly teeth but including centra of juveniles, small toe bones, and dermal ossifications. As with isolated bones, identifications are usually limited to the level of family; a great advantage of the study of dinosaurs through microfaunas is that the recovery of specimens from one or two days of careful sampling at a single site can equal or exceed the number of skeletons collected over a period of 70 years! Thus, microfaunas may prove to be very significant contributors to our knowledge of paleoecology of the Park. Accordingly, data recovered from a survey of 9 microfaunal sites in the Park (Dodson, study in progress) are incorporated into this review. Their use in this context is novel, and their suitability may be judged by the reader.

The Oldman Dinosaur Local Fauna

Articulated dinosaur specimens from the Park have been censused by Russell (1967) and Béland and Russell (1978). The latter display data in two ways: total dinosaur fauna (Table 1); and dinosaur megafauna, excluding dinosaurs of small or moderate size whose adult size did not exceed 100 kg (small theropods, ornithomimids, pachycephalosaurids). Of the dinosaur megafauna, hadrosaurs constitute 50.0%, ceratopsians 27.2%, ankylosaurs 14.6%, and tyrannosaurids 8.3%. Either way, hadrosaurs dominate, followed by ceratopsians.

Table 2 represents an attempt to summarize salient aspects of the record of articulated dinosaur specimens from the Park.

Table 1. The Dinosaur Census Based on Articulated Specimens Compared with the Census Based on Nine Microfaunal Sites

	Articulated (%)	Microfauna (%)
Hadrosaur	41.0	47.0
Ceratopsian	22.3	21.4
Ankylosaur	11.9	13.2
Pachycephalosaur	10.0	--
Small Theropod	3.2	5.5
Ornithomimid	4.8	2.2
Tyrannosaur	6.8	10.7
	N = 310	N = 1133

Data for articulated specimens taken from Béland and Russell (1978, Table 4); microfaunal data based on original collections made in 1980 and 1981.

Hadrosaurs

By any census technique, in any taphonomic mode, hadrosaurs dominate the fauna, and lambeosaurines, the hooded or crested duck-bills, dominate the hadrosaurines or flat-heads, by a factor of at least two to one. Lambeosaurines are known elsewhere from Montana, New Mexico, Utah, Baja California, Japan, Mongolia, China, and Russia (Weishampel and Weishampel, 1983). However, except for the Horseshoe Canyon Formation (or Member B of the Edmonton Formation) (Russell, 1967; Russell and Chamney, 1967), nowhere else do they dominate faunal assemblages. A strong case may be made for environmental control of hadrosaur distribution. In the Maastrichtian of central Alberta, the flat-head Edmontosaurus dominates the fauna of the deltaic, estuarine coal-swamps of the lower Horseshoe Canyon Formation that resemble the Judith River (Oldman). At the Park, however, no such zonation has yet been detected.

Corythosaurus and Lambeosaurus

Almost one in every seven dinosaur specimens found at the Park is referable either to Corythosaurus or to Lambeosaurus. Juveniles and subadults are known for both. Seven individuals of the genus Procheneosaurus have been

Table 2. Analysis of the Fossil Record of Currently Recognized Genera of Dinosaurs at Dinosaur Provincial Park

	Describer	Number of Specimens	Complete Skeleton Known?	Skull Known?	Size Range
Hadrosaurinae					
<u>Corythosaurus</u>	Brown, 1914	24	yes	yes	juvenile-adult
<u>Lambeosaurus</u>	Parks, 1923	18	yes	yes	juvenile-adult
<u>Parasaurolophus</u>	Parks, 1923	<u>1</u>	no	yes	adult
Subtotal lambeosaurine		43			
Hadrosaurinae					
<u>*Hadrosaurus</u> ¹	Leidy, 1858	10	yes	yes	juvenile-adult
<u>Prosaurolophus</u>	Brown, 1916	8	yes	yes	adult
<u>Brachylophosaurus</u>	Sternberg, 1953	<u>2</u>	no	yes	adult
Subtotal hadrosaurine		20			
Total hadrosaur		63			
Ceratopsidae					
<u>Centrosaurus</u>	Lambe, 1904	25 ²	yes	yes	juvenile-adult
<u>Chasmosaurus</u>	Lambe, 1914	20	yes	yes	adult
<u>*Monoclonius</u>	Cope, 1876	6	no	yes	adult
<u>Styracosaurus</u>	Lambe, 1913	12 ³	yes	yes	adult
<u>Eoceratops</u>	Lambe, 1915	<u>3</u>	no	yes	adult?
Total ceratopsian		66			
Ankylosauridae					
<u>Euoplocephalus</u>	Lambe, 1910	24	yes	yes	adult

Nodosauridae

<u>Panoplosaurus</u>	Lambe, 1919	7	yes	adult
Total ankylosaur		31		

Pachycephalosauridae

<u>Stegoceras</u>	Lambe, 1902	37	yes	juvenile-adult
<u>Gravitholus</u>	Wall and Galton, 1979	1	yes	adult
* <u>Pachycephalosaur</u>	Brown and Schlaikjer, 1943	1	yes	adult?
New form	Galton and Sues, 1983	3	yes	adult?
Total pachycephalosaurid		42		

Coeluridae

<u>Macrophalangia</u>	Sternberg, 1932	1	no	adult
<u>Dromaeosaurus</u>	Matthew and Brown, 1922	2	yes	adult
<u>Stenonychosaurus</u>	Sternberg, 1932	5	yes	adult
<u>Saurornitholestes</u>	Sues, 1978	2	yes	adult
<u>Chirostenotes</u>	Gilmore, 1924	1	no	adult
<u>Caenagnathus</u>	Sternberg, 1940	1	no	adult
Total coelurid		12		

Ornithomimidae

<u>Struthiomimus</u>	Osborn, 1917	9	yes	subadult-adult
* <u>Ornithomimus</u>	Marsh, 1890	1	no	adult
* <u>Dromiceiomimus</u>	Russell, 1972	1	yes	adult
Total ornithomimid		11		

Tyrannosauridae

* <u>Albertosaurus</u>	Osborn, 1905	14	yes	subadult-adult
<u>Daspletosaurus</u>	Russell, 1970	4	yes	adult
Total tyrannosaurid		18		

Notes to Table 2

Numerical data derived from Béland and Russell (1978) supplemented by recent finds by field parties of the Provincial Museum of Alberta, as discussed in the text.

- 1 Kritosaurus Brown, 1910, has been synonymized with Hadrosaurus Leidy, 1858 (Baird and Horner, 1977).
- 2 This figure does not include 38 individuals from bonebed 143 that probably are referable to Centrosaurus (Currie, 1981).
- 3 This figure includes seven specimens from a bonebed (Currie, 1981).

* Denotes a genus originally described from another locality; all other taxa were initially described from specimens collected at Dinosaur Provincial Park.

recognized as juveniles and subadults of these genera, P. erectofrons and P. cranibrevis being referred to Corythosaurus, P. praeceps to Lambeosaurus (Dodson, 1975). Skulls of these juveniles range from one-third to two-thirds the lengths of skulls of maximum adult size; skeletons of these young individuals are not common, but the skulls suggest that body lengths would have ranged from 3 to 6 m (adult lengths to 10 m). Subadults are recognized among the named "species" of Corythosaurus: C. brevicristatus is a young C. casuarius and C. frontalis is a young Lambeosaurus 80% of adult size. Of skulls in the top 20% of the size range, two patterns of crest are recognized in Corythosaurus and two in Lambeosaurus. Variability is confined primarily to a vertical solid plate of bone that surmounts the skull, including its muscular and respiratory components. The nature of this conspicuous plate of bone invites comparison with showy display structures such as coxcombs, dewlaps, and feathers; a sexual interpretation has been advanced to account for the equable dimorphism found in both genera (Dodson, 1975). According to this interpretation, specimens referred to Corythosaurus casuarius represent males of the species and those referred to C. intermedius, C. excavatus, and C. bicristatus represent females. Mature males are characterized by crests that are longer, taller, and fuller than those of females. Analogously, two species of adult Lambeosaurus reduce to a single, sexually dimorphic species. The male form, L. lambei, is characterized by a strong caudally-directed prong; the female form, L. clavinitialis, lacks the prong and has a lower crest. Dodson (1975) recognized six males and eight females among the specimens of Corythosaurus available to him, and six males and six females of Lambeosaurus.

L. magnicristatus presents a special problem. This Lambeosaurus is represented by only a single specimen from the Park, and by a second specimen from Manyberries, 200 km to the south. Its exceptionally tall, full crest marks it as a distinctive species, which was apparently rare in habitats represented by sediments at the Park. Parasaurolophus is another hadrosaur that was rarely preserved at the Park; only a single specimen is known, two-thirds of a skeleton including a magnificent skull 1.6 m (5.25 ft!) long. Elsewhere, this distinctive hadrosaur is known from several skulls from New Mexico (Ostrom, 1961a; Lucas, 1981) and one from Utah (Weishampel and Jensen, 1979).

Hadrosaurines

Hadrosaurines or flat-heads are preserved with only about half the frequency of lambeosaurines at the Park, although elsewhere they usually dominate. Prosaurolophus and Hadrosaurus (= Kritosaurus according to Baird and Horner, 1977) are by no means uncommon, whereas Brachylophosaurus is essentially known from only two skulls. A juvenile specimen of Hadrosaurus has been described (skull length 330 mm, 40% of adult size) by Waldman (1969). In general, however, juvenile hadrosaurines appear to be much less common than juvenile lambeosaurines.

Preservation

Preservation of hadrosaurs spans the spectrum of completeness (Dodson, 1971). The best specimens are among the finest dinosaur specimens known from anywhere in the world. No mummies are known, although patches of skin impression along the flank or tail are not unusual. Corythosaurus casuarius AMNH 5240 (type) is a superb skeleton 9.5 m long, complete from the snout to the tip of the tail (with extensive skin impressions). C. casuarius AMNH 5338 (plesiotype) is

slightly less complete, lacking the distal part of the tail, the left manus, and a few phalanges of the right manus; however, it presents extraordinary fine details including a stapes (Colbert and Ostrom, 1958) and the sclerotic ring of the eye (Ostrom, 1961b). Many skeletons are "headless wonders," and some isolated skulls are known. Specimens occur in all stages of disarticulation, and isolated bones are abundant in the badlands. One very small hadrosaurine skull (length 80 mm) was described by Sternberg (1955). Juvenile hadrosaur materials show up with regularity (although low frequency) in microfaunas. These finds include centra, edentulous jaws with as few as 10 tooth positions (compared to 40 or more in adults), and, rarely, small limbs down to 120 mm length (ROM 5577).

It was at one time suggested (Russell, 1967) that hadrosaurs were under-collected and, therefore, under-represented in census counts relative to other dinosaurs. It is now clear (Béland and Russell, 1978) that such a correction is unnecessary. The abundance of hadrosaur teeth in microfaunas (Table 1) relative to remains of other dinosaurs corresponds closely to that reported in dinosaur census counts (Russell, 1967; Béland and Russell, 1978). This further reinforces the concept that no correction of count data is required.

Ecology

The nature of the niche separation between hadrosaurines and lambeosaurines is not clear. Both included animals 8 to 10 m long and almost 2½ m high at the hips. Hadrosaurines tended to be a little stockier of build, with shorter distal segments of the forelimb than in lambeosaurines. Hadrosaurine skulls attained a meter in length and had widely flaring premaxillary "beaks" or duck bills, while lambeosaurine skulls usually did not exceed 750 mm in length and had narrower beaks. In Parasaurolophus, the skull was 800 mm long, exclusive of the plume-like crest.

The duck-like beak, webbed manus and teeth, erroneously believed by Cope to be weak, suggested anatomical adaptations to aquatic or amphibious habits (Brown, 1914a; Lull and Wright, 1942). Ostrom (1964a) pointed out numerous anatomical traits suggestive of life on land; these include general structure of the trunk and limbs (amplified by Galton, 1970a), the characteristic strengthening of the vertebral column from mid-thorax to mid-tail with the criss-crossing trellis of ossified tendons of the deep epaxial muscles, and the existence of a complex, robust dentition quite capable of reducing the toughest land plants. Hadrosaurs had unique, complex masticatory systems (Weishampel, 1981a) that were capable of reducing plant material of almost any conceivable physical consistency. Ostrom reviewed the botanical record and reported a preponderance of terrestrial plants in the Judith River (Oldman) and noted the report of Krausel (1922) of conifer material in the stomach of an Anatosaurus mummy from Wyoming. New botanical data have recently been presented by Jarzen (1982), who recognized 85 species of palynomorphs that represent mosses, hornworts, lycopods, ferns, cycads, conifers, and flowering plants; lower plants comprise 38.8% of the species, gymnosperms 14.1%, angiosperms 43.5%, and unidentified 3.6%. The plants suggest a tropical, wet lowland. Dodson (1971) documented the overwhelming statistical tendency of hadrosaur skeletons to be found in channel deposits rather than in overbank or floodplain deposits; from this he concluded that hadrosaurs died and probably lived in or near rivers.

Although the conclusion may or may not be correct, Behrensmeyer (1975) pointed out that it was not justified by the evidence; for instance, drowning during river crossing (as wildebeest do today in Africa) represents an excellent mechanism for preservation of complete skeletons.

A synthetic view of hadrosaur ecology at the Park takes into account that the climate was humid and that water was abundant. River channels were a major feature of the landscape, as were ponds and lakes. Plant productivity was high, both on land and in the water. Hadrosaurs were the dominant herbivores. Their potential vertical feeding heights ranged from ground level to $4\frac{1}{2}$ m (15 ft). They probably consumed low-growing herbaceous vegetation as well as leaves and twigs of trees. It is unlikely that conifer needles played a very large dietary role for hadrosaurs. Pollen analysis (Jarzen, 1982) suggests that they were not very abundant, and the chemical defenses of noxious pine leaves discourage almost all would-be herbivores today; dominant hadrosaurs are unlikely to have subsisted on such a marginal food source in normal times. It is no coincidence that the peak of ornithischian diversity coincides with the diversification of the angiosperms; for hadrosaurs, flowering plants were the solution, not the problem! Hadrosaurs were well adapted for life on land and may have fed largely or exclusively there. Water was also an important part of their habitat, and there is every reason to believe they probably made extensive use of it. It is not possible to assess the relative importance of various behavioral motivations, but potential uses of water include predator avoidance, thermoregulation, transportation, and even preferred food items such as lush seasonal water plants. Tendons on the tail resisted bending in the dorsoventral plane, but depending on how they attached to the column, may not have seriously damped lateral sculling movements of the deep tail; they could also have been powerful leg swimmers. It requires much more ingenuity to conceive of the function of a broad beak and webbed manus on land than in the water. In summary, hadrosaurs were probably neither strictly terrestrial nor strictly aquatic, but moved readily between land and water.

Hadrosaurs evidently had keen sense of sight and hearing, as determined by studies of endocranial casts (Ostrom, 1961b; Hopson, 1979). Eye size was very large, as inferred from the diameter of sclerotic rings (70 mm for Corythosaurus; 88 mm for Saurolophus). With such large eyes and the apparent use of sexually dimorphic visual display structures (Dodson, 1975; Hopson, 1975), it would seem that speculation about the possibility of color vision and vivid color displays is not altogether unwarranted. Auditory centers of the brain were well developed and a good functional stapes was present. Hopson (1975) interpreted aspects of the narial region of the snout and of the crest as potential vocal resonating structures. Weishampel (1981b) investigated the lambeosaurine narial passages as a paradigm for acoustic resonating structures; he discovered resonant frequencies of 48 to 240 Hz for Parasaurolophus, with harmonic modifications up to 919 Hz. Smaller lambeosaurines, particularly juveniles, would have produced high-frequency sounds (juvenile alligators vocalize to adults at up to 2000 Hz). The low-frequency sounds of adult hadrosaurs have favorable properties for communication over long distances through varied habitats.

The role of olfaction in hadrosaurs is more ambiguous. Ostrom (1961b) argued for a predominantly olfactory function of the lambeosaurine crest, but this is neither corroborated by endocranial anatomy (olfactory tracts of

archosaurs are not confined by bone) nor sufficient to explain variability of the crests, particularly the non-narial, coxcomb portion. In summary, hadrosaurs may have had a keen sense of smell, but it is neither confirmed nor disproven by the evidence.

Ceratopsians

Ceratopsians were dentally-sophisticated, four-footed herbivores with large heads, elaborate frills, and various patterns of horns over nose, eyes, and frill. They were the second most common group of dinosaurs in the Park, consistently occurring at about half the frequency of the hadrosaurs. No primitive ceratopsians are known from the Park, although such ceratopsians are known from the Horseshoe Canyon, Hell Creek, and Two Medicine Formations. Judithian ceratopsians fall into either the long-squamosaled group (Chasmosaurus, Eoceratops) or the short-squamosaled group (Centrosaurus, Monoclonius, Styracosaurus). Based on the record of single specimens, Chasmosaurus and Centrosaurus appear to have been about equally common, and both about as abundant as Corythosaurus and Lambeosaurus (Table 2). Centrosaurus, however, also occurs in bonebeds. At quarry 143, 51 individuals have so far been identified on the basis of braincases (Currie, 1981; pers. comm., 1982).

Ceratopsians were abundantly preserved, with many excellent, complete skulls (e.g., Lull, 1933). Morphological variability is high; seven species of Centrosaurus have been described from the Oldman local fauna, as well as four species of Chasmosaurus. It is a certainty that a modern study of morphological variability (e.g., Dodson, 1975, 1976) of these taxa would result in a much more satisfactory taxonomic picture; sexual dimorphism is probably a major feature of variability. Such a study has not yet been done. Lull's 1933 review of the Ceratopsia was inadequately illustrated to facilitate such a needed study. Any species count of Judithian ceratopsians is presently meaningless at our current state of knowledge. A further source of confusion and/or controversy concerns the identity of the genera Monoclonius and Centrosaurus. Monoclonius was named by Cope (1876) from the Judith River Formation of Montana while Centrosaurus was named by Lambe (1904) from Alberta. Brown (1914b) synonymized the two, while Lull (1933) sat on the fence, referring to Alberta specimens as Monoclonius (subgenus Centrosaurus). Although many authors (e.g., Steel, 1969) have followed Lull, Lull himself was by no means certain; the differences in the crest "are, to my mind, a serious obstacle to the acceptance of generic identity" (Lull, 1933, p. 82). Lull believed that Monoclonius was restricted to Montana and Centrosaurus to Alberta. However, each is now known in the other's domain (Sternberg, 1938, 1940; Russell, 1967). Monoclonius lacks orbital horn cores and the hook-like processes so characteristic of the caudal border of the frill of Centrosaurus. Monoclonius is uncommon in sediments at the park, although apparently there is a Monoclonius bonebed (Currie, 1981).

Styracosaurus is the most distinctive of Judithian ceratopsians, with its strongly-spiked frill. It is also very uncommon, referred articulated material consisting of a single excellent skull and skeleton (type of S. parksi), a skull lacking jaws (type of S. albertensis), and an incomplete skull. However, a Styracosaurus bonebed contains the disarticulated remains of at least seven individuals (Currie, 1981). Eoceratops remains the most problematic of Oldman ceratopsians, with three referred specimens, the type being a rather fragmentary skull, the second specimen (Gilmore, 1923) a fairly good, articulated skull. A third skull recently has come from the Centrosaurus bonebed. The relatively small size of the skull (estimated length 1 m, as compared with 1.2 to 1.5 m for large Centrosaurus) invites the interpretation that Eoceratops is a subadult

of Chasmosaurus. However, recent restudy of this material (Tyson, 1977) suggests that the genus is valid.

Chasmosaurus had the largest skull of Judithian ceratopsians, with lengths approaching 2 m. It was the only common long-frilled ceratopsian in the Park; while it is among the most common dinosaurs found as single specimens, it does not appear to be a common constituent of bonebeds.

Preservation

Remains of ceratopsians are very abundant, and excellent material is available that includes both skulls and skeletons. Béland and Russell (1978) pointed out that complete skeletons, or even half-complete skeletons of ceratopsians, occur at a much lower frequency than do hadrosaurs: half of the hadrosaur material they document is either "complete" or "half-complete," while only a quarter of the ceratopsian material falls into these categories. Isolated skulls correspondingly are a more important mode of preservation for ceratopsians. This taphonomic contrast may be important evidence of contrasting habitat preferences with hadrosaurs. Articulated juvenile and subadult material, uncommon for hadrosaurs, is extremely rare for ceratopsians. Ceratopsian teeth are important components of Oldman local microfaunas, and their abundance relative to hadrosaur teeth closely mirrors the relative abundances of these animals as determined by census of articulated materials (Table 1). A very important characteristic of ceratopsians is their tendency for monospecific dominance of bonebeds. Thus, separate bonebeds within the Park are dominated by Centrosaurus, Monoclonius, and Styracosaurus (Currie, 1981). This tendency continues elsewhere, as for instance the Pachyrhinosaurus bonebed at Scabby Butte (Langston, 1976). Thus, a ceratopsian bonebed is characterized by low taxonomic diversity, with a single kind dominating. By contrast, hadrosaur bonebeds are characterized by the presence of all kinds of dinosaurs.

Ecology

Judithian ceratopsians were bulky four-footed herbivores that attained lengths of 5 m or so. Their remains are found in abundance in channel deposits, in environments similar to those in which hadrosaurs are found. However, the taphonomic contrast in their state of preservation noted above may encourage the interpretation that ceratopsians favored dry ground (i.e., river banks, flood plains) to a somewhat greater degree than did hadrosaurs. Those few dinosaur specimens found in overbank deposits tend to be ceratopsians (Dodson, 1971). Ceratopsians and hadrosaurs frequented the same general habitats, but may have used the habitat differentially in ways that cannot now be determined. Ceratopsian jaw mechanics have been analyzed by Ostrom (1964b, 1966). Ceratopsians had complex dental batteries that were powered by immensely strong jaw muscles but which seemingly lacked the versatility of hadrosaur jaws. The occlusal plane of ceratopsians lay in a vertical plane, permitting shearing and chopping, but seemingly allowing no crushing and grinding that one would expect of a herbivore. Ostrom thus postulated an extremely tough, fibrous diet for ceratopsians, consisting perhaps of cycads or palms (neither of which is known from the Park). What they ate is not clear, but they were more limited in their vertical feeding range than were hadrosaurs, their reach off the ground being a meter or less.

The tendency of ceratopsians to occur in bonebeds dominated by single genera, in contrast to other Judithian dinosaurs, encourages the view that they may have been herd-dwelling animals. Farlow and Dodson (1975) interpreted the horns and frills of ceratopsians as display organs facilitating species recognition and mediating intraspecific interactions among males. According to this model, long-frilled ceratopsians with prominent, paired orbital horns (e.g., Chasmosaurus) would have been gregarious animals that resolved male combat without serious injury to rivals. In contrast, short-frilled ceratopsians with a single prominent nasal horn (e.g., Centrosaurus) would have engaged in more injurious combat, in consequence of which males at least would have been less gregarious. The tendency of Centrosaurus to occur in bonebeds does not encourage belief in the dichotomy between solitary and gregarious habits; however, patterns of aggregation and dispersal may have had a seasonal basis as well.

Ankylosaurs

Ankylosaurs represent only about 12% of the dinosaur fauna preserved in the Park. They were of moderate to large size, broad, short-limbed, and heavily armored. They are regarded as among the most primitive of dinosaurs despite their late occurrence in time. Their imperforate acetabulum may represent the retention of a thecodont character otherwise unknown among dinosaurs. They were herbivores (or omnivores; Maryanska, 1977) characterized by small, simple teeth, few in number and neither interlocking to form a battery nor aligned to form a single cutting edge (Coombs, 1978a). A unique character was an elaborate body armor consisting of ordered rows of oval keeled scutes, between which are large numbers of very small, irregular ossicles.

At least five different names have been proposed for Judithian ankylosaurs, but only two are currently recognized: Euoplocephalus (= Dyoplosaurus, Scolosaurus), Family Ankylosauridae, and Panoplosaurus (= Edmontonia), Family Nodosauridae (Coombs, 1978a). As representative of two clearly differentiated families, the two genera are distinguished by a long list of features, among which are the following: Euoplocephalus had a wide skull with laterally projecting spines at the back corners; cranial sinuses and complex narial passages were present; dermal scutes of the dorsal armor had hollow bases; and a tail club was present. Panoplosaurus had a comparatively narrow skull lacking lateral processes; narial passages were simple and straight; cranial sinuses were absent; dermal scutes had solid (or slightly concave) bases; and a tail club was lacking. Béland and Russell (1978) documented 24 articulated specimens of Euoplocephalus and only 7 of Panoplosaurus; however, tail clubs as isolated specimens are extremely uncommon, and dermal scutes of the ankylosaurid type are very much less common as isolated specimens than are the nodosaurid type.

Preservation

Béland and Russell (1978) record 37 specimens of ankylosaurs; of these a mere three are complete, 11 are "half-complete," and the balance are fragmentary, including 9 isolated tail clubs. These authors compared the poor representation of complete ankylosaurs with that of ceratopsians and contrasted it with the high representation of complete hadrosaurs and inferred postmortem transport before burial. As with ceratopsians, it could also indicate greater preference for terrestrial environments than hadrosaurs had. Ankylosaur remains, principally teeth and dermal ossicles, are consistently found in microfaunas. They generally account for 5-13% of the identifiable dinosaur material, but at two sites they account for 24 to 29%.

Ecology

Ankylosaurs are not well understood from an ecological point of view. Heavy armor and short limbs suggest slow-moving habits. Small, rather than weak teeth (despite body weights estimated at two to three tons) and low vertical feeding range suggests that comparatively soft, possibly aquatic vegetation served as major food. Maryanska (1977) argues for the inclusion of insects and larvae in the diet, a suggestion that is not implausible. Russell (1977) speculated: "It is difficult to image the creatures feeding on anything except delicate or pulpy objects near the surface of the ground. Perhaps they browsed on ferns, lilies and arum plants growing in shaded areas, or pulled cattail tubers from the moist soils of the marshes."

Pachycephalosaurs

Pachycephalosaurs are small, bipedal ornithopods characterized by enormously thickened fronto-parietal portions of the skull. The name literally means "thick-headed lizards." Four genera are reported from the Oldman local fauna. Stegoceras is the best known of these, being represented by a partial skeleton, including skull and jaws (Gilmore, 1924), as well as by numerous isolated partial crania (Wall and Galton, 1979; Chapman *et al.*, 1981). Gravitholus (Wall and Galton, 1979) is a unique specimen having either a very wide skull or a very small brain. Pachycephalosaurus has been recognized recently for the first time based on a single fragmentary cranial specimen (Wall and Galton, 1979); otherwise, it is known from the Lance Formation of Wyoming and Montana. The most recent to be described is a flat-headed pachycephalosaurid similar to Homalocephale of Mongolia (Galton and Sues, 1983). Stegoceras was a small animal with a skull 20 cm long and a total body length of barely more than 1 m. Within the past decade pachycephalosaurs have come to be known worldwide, specimens now being known from England (Galton, 1971), Madagascar (Sues and Taquet, 1979), and Mongolia (Maryanska and Osmolska, 1974). Mongolian Prenocephale seems intermediate in cranial morphology between Stegoceras and Pachycephalosaurus.

Chapman *et al.* (1981) performed a biometric analysis on 23 Stegoceras crania from the Park and inferred sexual dimorphism on the basis of their analysis. The sample included 10 males and 13 females, the former distinguished by larger and somewhat thicker domes.

Preservation

As articulated specimens, pachycephalosaurids are exceedingly rare, only a single skull and skeleton being known. Isolated crania, sometimes water-worn, sometimes not, are uncommon but are presently found consistently at the rate of perhaps two per field season. In fact, in terms of identifiable specimens, Stegoceras ranks (anomalously) as the most abundant of the 28 genera of Judith River (Oldman) dinosaurs! Pachycephalosaurid remains are not recognized in micro-faunas, although their teeth might be dismissed as those of ankylosaurs. Béland and Russell (1978, Table 4) record pachycephalosaurids as constituting 10% of the total dinosaur fauna; intuitively I would regard this figure as at least three times too abundant. Nonetheless, such a figure underscores the fact that they were not so much rare animals as that destructive processes acted against them due to their small size. Thus the fossil record is strongly biased against articulated remains of Stegoceras, as well as other small dinosaurs (see discussions of small theropods, ornithomimids, and crocodiles below).

Rather little has been ventured about the food habits of pachycephalosaurids. They were small herbivores or omnivores with simple teeth of primitive aspect. Such teeth would have been suitable for leaves, fruits, seeds, and insects (Maryanska and Osmolska, 1974). They are regarded as having had good senses of vision and smell. The function of the thickened dome has attracted the most speculation. Galton (1970b, 1971) has made a strong case for male combat, involving the clashing of lowered head in a ram-like fashion. Analysis of neck musculature and stress distribution through the skull (Sues, 1978a) and of sexual dimorphism (Chapman *et al.*, 1981) has supported this suggestion.

Small Theropods

Small theropods constitute a very important part of the Oldman dinosaur local fauna. They were diverse but neither abundant nor well preserved. According to Béland and Russell (1978), they account for 3.2% of the articulated dinosaur fauna of the Park, but in microfaunas they averaged 5.5% of the total dinosaur component. No fewer than six genera have been described, not one based on anything resembling a complete skeleton. Caenagnathus (Sternberg, 1940) is based only on a single jaw, the dinosaurian nature of which was in dispute until a similar jaw was recognized in Oviraptor from Mongolia (Osmolska, 1976). Chirostenotes (Gilmore, 1924) is based upon a pair of tridactyl hands; Macrophalangia (Sternberg, 1932) is based upon a single foot. A partial skeleton discovered by the Tyrrell Museum of Paleontology in 1979 may possibly relate these two genera. Saurornitholestes (Sues, 1978b) is based on very incomplete cranial, vertebral, and forelimb material. Dromaeosaurus (Matthew and Brown, 1922) is known from a superb skull with jaws plus a few foot bones, among which is the enlarged, sickle-shaped, trenchant claw of the second toe that is so characteristic of Deinonychus and its relatives. It was recognized to be closely related to Lower Cretaceous Deinonychus of Montana (Colbert and Russell, 1969; Ostrom, 1969).

Stenonychosaurus (Sternberg, 1932) is the most completely characterized of the small theropods, as well as the most common of these. Nonetheless, the best specimen (Russell, 1969) consists only of an incomplete skull including part of the braincase, four vertebrae, four ribs, two ulnae, one proximal radius, one carpal, three phalangeal fragments, a femoral shaft, tarsal fragments, one good metatarsal plus fragments of others, and 14 phalanges. Stenonychosaurus appears closely related to Saurornithoides from Mongolia. Only Dromaeosaurus and Saurornitholestes have associated teeth; however, at least three different types of small theropod teeth are known from the Oldman.

Preservation and Ecology

Articulated remains of small theropods are extremely rare, with only a single good skull, that of Dromaeosaurus, and no complete skeleton. It does not follow that small theropods themselves were extremely rare, and there is ample reason to believe that this was not the case. Russell (1969) reports that in six weeks of field work a small field party recovered 58 isolated bones of small theropods (order of frequency: Stenonychosaurus, Dromaeosaurus, Chirostenotes). In nine microfaunas that I collected and examined from all over the Park (Dodson, in prep.), small theropods were ubiquitous and remarkably consistent. Identifiable remains include teeth, vertebrae, metapodials and phalanges. They averaged 34% of the total theropod component but never went lower than 20%. It is not their rarity that led to their infrequent preservation as articulated materials but their small size. There is an intense taphonomic bias in the Oldman local fauna against preservation of skeletons of animals of small size. Size-related preservational biases have been documented in East Africa (Behrensmeyer *et al.*, 1979). A consideration of the fossil record of crocodilians provides perspective. No one would consider crocodilians as rare in

the Park; their remains are ubiquitous, abundant, and conspicuous. They account for nearly 11% of all materials in the microfaunas; their contribution to the mesoreptile component of the fauna (i.e., turtles, champsosaurs, crocodiles) averages 26% and is never lower than 16%. Yet as articulated specimens, crocodiles too are extremely rare. Only a single articulated partial skeleton is known from the Park, and perhaps 10 partial to complete skulls. Neither small theropods nor crocodiles were rare in any meaningful sense, but both belong to a size component against which the fossil record discriminates strongly.

As Judithian small theropods are incomplete, their sizes are best determined by comparisons with Lower Cretaceous Deinonychus which is exquisitely preserved. Deinonychus had a skull length estimated at 320 mm, a body length of 3 m, a height of less than 1 m at the hips, and an estimated weight of 60 to 70 kg, about that of a man (Ostrom, 1969). Dromaeosaurus had a skull length of 234 mm (Colbert and Russell, 1969), and Saurornithoides, morphologically very close to Stenonychosaurus, had a skull length of 216 mm (Russell, 1969). Accordingly, Judithian small theropods appear to have been more like 2 m in length, half a meter in height, and 20 to 30 kg in weight--small indeed! (Russell and Séguin, 1982, have recently reconstructed Stenonychosaurus with a length of about 3 m and a weight of around 40 kg.) Nonetheless, tiny Velociraptor from Mongolia evidently preyed on Protoceratops (Kielan-Jaworowska, 1975), and the repeated association of Deinonychus teeth with Tenontosaurus skeletons suggests a predatory-prey relationship despite a marked disparity in size. With sharp teeth and slashing claws on the feet, a ferocity like that of shrews, weasels, or wolverines, driven by the urgency of high gram-metabolic rates, comes to mind. Russell (1969) noted a very large endocranial (brain) volume in Stenonychosaurus and inferred bird-like intelligence and excellent vision (see also Hopson, 1977, 1979); he suggested that they were well adapted to feed on small, possibly crepuscular mammals. The more robust Dromaeosaurus perhaps concentrated on small ornithischian prey as did Deinonychus.

Ornithomimids

Ornithomimids were theropods of intermediate size, up to 3.5 m long and 1.5 m at the hips, long-legged, slender of build, with long necks and small, toothless skulls. In the most recent review of ornithomimids, Russell (1972) recognized three genera from the Oldman local fauna. Struthiomimus is the common form, with eight partial and one complete articulated specimens; Ornithomimus and Dromiceiomimus are represented by single specimens each. Distinctions among genera are not based on skulls, which are rare, fragile, and poorly preserved, but on skeletal ratios and the structure of the hand. Briefly, Dromiceiomimus is the longest limbed, most cursorial of the Judithian ornithomimids, but its hand is not known. Struthiomimus is characterized by the robust build of the forelimb, which includes digits of unequal lengths equipped with powerful, strongly recurved claws. Ornithomimus has a forelimb of more gracile construction, with digits of equal lengths and claws of lighter build and straighter aspect. Nicholls and Russell (1981) cautioned that proportional differences are based on few specimens (three or fewer) and could have an allometric basis; in default of better specimens, these diagnoses must stand.

Preservation

The comparatively small size, lightness of construction, and hollowness of bones have conspired to produce a poor fossil record as was the case for small theropods. Indeed, only two complete skeletons of ornithomimids are known from North America (Nicholls and Russell, 1981), one of which comes from the Park. Even when articulated materials are found, crushing of the fragile bone is a

major problem, particularly for skulls. As articulated specimens, ornithomimids constitute 4.8% of the Oldman dinosaur local fauna (Béland and Russell, 1978) but account for only 2% of the dinosaur component of the microfaunas. Moreover, they were not recorded in four of nine microfaunas. Absence of teeth, which constitute over half of all microfaunal remains in the Park, contributes significantly to the bias against ornithomimids in the microfaunal record. Otherwise, ornithomimids are recognized on the basis of vertebrae and unguals, both of which appear in the microfaunas.

Ecology

Reconstructions of the biology of ornithomimids have focused on such anatomical features as the long limbs, large eyes, and toothless jaws, all of which invite comparison with ostriches, which they resemble in size and shape. (The name Struthiomimus means "ostrich mimic.") In a biomechanical analysis of Dromiceiomimus hindlimbs in comparison with Recent Struthio, Russell (1972) concluded that the ornithomimids could run faster than ostriches but with less maneuverability. Coombs (1978b) inferred that ornithomimids were the swiftest of dinosaurs (97 km/hr for Dromiceiomimus) but were not quite as fast as ostriches. In the absence of teeth, a relatively soft, protein-rich diet is inferred; eggs, insects, larvae, fruits, lizards, even carrion perhaps (vulture-like) are all possibilities. Long forelimbs were involved in food capture or acquisition; robust Struthiomimus probably actually dug or rooted for food, while gracile Ornithomimus was unlikely to have done so. Brain size of ornithomimids was very large, comparable to that of ostriches (Russell, 1972; Hopson, 1977, 1979). The eyes were enormous, with an orbital rim measuring 72 mm in Dromiceiomimus, suggesting an eye larger than that of any living terrestrial vertebrate. Vision thus was acute.

Carnosaurs

The ultimate carnivores at the top of the trophic structure of the Judithian dinosaur community were the carnosaurs Albertosaurus (Osborn, 1905) = Gorgosaurus (Lambe, 1914) and Daspletosaurus (Russell, 1970). The shape of these predatory bipeds is highly characteristic: very large heads, short necks, extremely short forelimbs with only two digits (a characteristic of the Family Tyrannosauridae), long hindlimbs and tail. Daspletosaurus torosus (whose name means "fleshy frightful lizard") attained the same overall length as Albertosaurus (8.5 to 9 m) and same skull size (1 m). Daspletosaurus was a bulkier, more stocky animal in many of its dimensions; for instance, it had a maximum breadth across the thorax of 1350 mm (Russell, 1970). In addition, the base of the tail was heavier, the femur more robust, the presacral vertebrae somewhat shorter, the humerus longer and more robust, the ungual of the first digit less curved. In Albertosaurus the two digits of the hand were gracile and parallel; in Daspletosaurus they were heavier and divergent. The teeth of Albertosaurus are smaller and diminish in size and robustness towards the back of the maxilla; those of Daspletosaurus are larger and are not reduced in size at the back of the toothrow.

Known specimens of Albertosaurus outnumber those of Daspletosaurus by a count of 14 to 4 (Béland and Russell, 1978). In addition, many subadult specimens of Albertosaurus are known, but none of Daspletosaurus have been discovered.

Preservation

Although carnosaurs are not common, a number of excellent articulated skeletons are known. Carnosaur teeth are also consistently found in microfaunas, being present in all nine sampled. Carnosaur teeth average 10.7% of all identified specimens in the microfaunas, and 58% of the theropod component. As with small theropods, tyrannosaurs are significantly enriched in the microfaunas as compared with their representation as articulated specimens.

Ecology

As ultimate carnivores of the Judithian large-vertebrate community, Albertosaurus and Daspletosaurus occupied the top of the trophic pyramid. Russell (1970) speculated that with its greater bulk, Daspletosaurus may have preyed preferentially on ceratopsians, Albertosaurus on hadrosaurs. Farlow (1976a) contrasted Jurassic carnosaurs feeding on sauropods that dwarfed them with Cretaceous carnosaurs feeding on prey to which they were nearly equal in body size; he speculated that tyrannosaurids were solitary carnivores, possibly capable of singly dropping prey animals. Of course it cannot be ruled out that the mighty tyrannosaurids were scavengers.

Bakker (1972, 1975, 1980) developed an ingenious argument in support of the concept of endothermy in dinosaurs, at least theropods. He pointed out that modern endotherms (i.e., birds and mammals) require approximately ten times more food for a given body size than do living ectotherms (e.g., snakes, lizards, crocodilians). He posited that the fossil record of theropods, especially of carnosaurs at Dinosaur Provincial Park, was consistent with the predictions of an endothermic model for dinosaurs. Data cited in support of this contention were the census data of Russell (1967). Using the same or emended data, Farlow (1976b, 1980) and Béland and Russell (1979) concluded that the actual proportion of tyrannosaurs as preserved is several times too great to support a model of large theropods as endotherms. This conclusion naturally is vigorously disputed by Bakker (1980).

Non-Dinosaurian Vertebrates

Many other kinds of vertebrates are preserved in abundance in the Judith River (Oldman) Formation at Dinosaur Provincial Park. It is beyond the scope of this paper to review this component in detail. However, the existence of the other vertebrates provides complementary information that is essential to the understanding of the overall community in which the dinosaurs lived. It is fair to say that the non-dinosaurian lower vertebrates are a seriously understudied component of the Judithian fauna. Non-dinosaurian vertebrates of the Oldman local fauna have not received the detailed analysis that certain other faunas have (e.g., Lance Formation, Wyoming: Estes, 1964; Hell Creek Formation, Montana: Estes and Berberian, 1970; Judith River Formation, Montana: Sahni, 1972). Mammals are among the rarest components but have been the best-studied (e.g., Fox, 1976, 1979a, b, c, 1980, 1981), although from other Judithian localities in southeastern Alberta.

So-called mesoreptiles (turtles, crocodiles, champsosaurs) are a very conspicuous component of the fossil record, and collectively amount to 39.9%

of the total microfauna (compared with 37.4% dinosaur and 23.1% fish). Béland and Russell (1978) record 89 articulated specimens of turtles in three families: Baenidae (Gaffney, 1972), Trionychidae, and Dermatemydidae. Judith River (Oldman) turtles were most recently reviewed by Nicholls (1972). Turtles themselves account for 19.0% of all microfaunal remains! Béland and Russell (1978) categorized trionychids and dermatemydids as aquatic and baenids as terrestrial; Nicholls (1972) regarded baenids as aquatic; Lucas (1981) called them semi-aquatic.

Crocodylians are very rare as articulated specimens but common as contributors of teeth, scutes, and centra to microfaunas. Champsosaurs, enigmatic aquatic eosuchians that were somewhat reminiscent of gavials in form, are even rarer as articulated skulls and skeletons, but are common as contributors of centra, limbs, girdle elements, and teeth. Champsosaurs were small animals, up to about 2½ m in length (Erickson, 1972); Judithian crocodylians were of similar size.

Fishes, too, are an important component of the fauna, although nearly completely ignored to date in systematic or faunal studies of the Oldman local fauna. The two most common fishes are the batoid, Myledaphus, and the gar, Lepisosteus. Centra of amiids and spines of sturgeon (Acipenser) are less common but are regularly found. Jaw fragments of the small, needle-nosed holostean Belonostomus are rare. It is probable that yet unidentified teleosts are represented by centra, but these have not yet been studied seriously. Lucas (1981) commented on the rarity of teleost remains in the Campanian of New Mexico. Shark teeth are very uncommon at the Park. At other sites in the Judith River Formation of southern Alberta and Montana, shark remains are both abundant and diverse. At a series of sites in north central Montana, Clemens and Goodwin (1981) report as few as one or as many as nine different genera of sharks. Presumably high diversity of sharks indicates estuarine conditions that did not prevail at the Park.

Snakes have not yet been reported from the Oldman local fauna; snake remains are generally very rare in the Cretaceous of western North America. Occasional lizard centra are found, usually referred to the varanid, Paleosaniwa. Rare frog material has not received generic assignment. Salamander material is fairly uncommon but is found at every microsite, averaging about 1% of the fauna. Centra and jaws are found, and are referred to Scapherpeton, Lisserpeton, and Prodesmodon.

Mammals are extremely rare at the Park. Two of 3732 specimens examined from 9 microfaunal sites are mammalian. One site in the Park, the "railroad grade," has yielded more than 500 specimens by surface-picking (comprising multituberculates and marsupials principally), but at no other site in the Park, despite moderately extensive search, have mammals been found in abundance. Other sites in southeastern Alberta, notably to the east and south of the Park, have yielded mammals more readily, as is apparently the case in north central Montana as well. Possibly, environments closer to the sea provided habitats more congenial either to the life of Cretaceous mammals or to their preservation.

Faunal Studies of the Judith River (Oldman) Formation: Present and Future

The badlands of the Judith River (Oldman) Formation exposed along the Red Deer River at Dinosaur Provincial Park are some of the most fossiliferous anywhere in the world. As a result of a 70-year history of intensive collecting

(estimated by Béland and Russell, 1978, to have exceeded 10,000 man-days of collecting effort by 1954!), the Oldman local fauna dinosaur community is the best-known in the world. Large field parties are once again working in the Park at a scale exceeding that of any time in the past. The Tyrrell Museum of Palaeontology of the Province of Alberta resumed work there in 1979, and by 1980 crews of up to 30 persons worked there for the summer. With such an intense rate of effort operating on a continuing basis, the present rate of discoveries promises to increase.

An obvious result of the renewed effort will be discoveries of fossils that are either extremely rare or presently absent. Trends have already appeared. The first pterosaur fragment from the Park was described in 1972 (Russell, 1972). By 1980, two more specimens had been found (Currie and Padian, 1983), including a huge partial femur possibly referable to Quetzalcoatlus (Currie and Russell, 1982). Further finds were made in 1981 and 1982, and further finds are to be expected now that a "search image" has materialized. As of yet, birds are still unreported. Plesiosaur remains have a nearly similar history of discovery. Apart from a partial specimen found very early (Lambe, 1902) and all but forgotten, plesiosaurs were almost completely overlooked. Then in 1979, a pair of pubes was found. In 1980, several phalanges were found at separate sites, and then finally a partial skeleton was located. Plesiosaurs thus have taken their part as a component of the Oldman local fauna.

Among dinosaurs, a surprising absence is that of hypsilophodonts. Parkosaurus and Thescelosaurus are known from the Edmonton Group but so far no trace has been found of such animals in the Oldman local fauna. Similarly, the primitive ceratopsian Leptoceratops comes from the Horseshoe Canyon and Brachyceratops from the Judith River and Two Medicine Formations of Montana. The apparent absence of such animals from the Park is anomalous, and future finds may be expected. Indeed, in 1982 a small, partial frill of a juvenile ceratopsian was found (Currie and Dodson, MS in prep.). This specimen may shed light on the question of whether Brachyceratops is a valid genus or a juvenile of Monoclonius (Dodson, in study).

The study of bonebeds will be an important aspect of future work in the Park, and data from them will be incorporated into a synthesis of Judithian paleoecology. Microfaunas may prove to be an extremely useful tool for interpretation of local environments within the Oldman ecological mosaic.

The Judith River Formation is widespread in southern Alberta, and is continuous with the lowland sediments of the same name to the south in central Montana, and with the upland Two Medicine Formation of western Montana to the southwest. Although no other site in Alberta or Montana appears to rival Dinosaur Provincial Park in richness of fossils, study of other important sites on the broad Judithian depositional surface promises to provide an unparalleled opportunity to reconstruct the paleoecology of the Cretaceous biota. The Tyrrell Museum has collected for several years at Sandy Point, 80 km east of the Park and presumably near the shoreline. Fox (1976, 1979b, c) has studied mammals from a variety of Judithian sites east and south of the Park (e.g., Hilda, Irvine, Manyberries). Clemens and Goodwin (Berkeley) currently have important faunal studies underway in Judithian near-shore sites in north-central Montana. Horner (Montana State University) is currently studying upland sites

in the Two Medicine of western Montana. Finds there include abundant egg-bearing nests and nestling hadrosaurs (Horner and Makela, 1979; Horner, 1982) and a dinosaur fauna whose aspect differs somewhat from that of lowland sites. When sites such as these have been fully documented, it will be possible to describe paleoecology of dinosaurs, mammals, and other components of the biota in ways that have not been possible by reference to widely separated sites over discontinuous surfaces (e.g., Lucas, 1981).

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